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SERENGETI WILDEBEEST MIGRATORY PATTERNS MODELED FROM RAINFALL AND NEW VEGETATION GROWTH

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Abstract. We used evolutionary programming to model innate migratory pathways of wildebeest in the Serengeti Mara Ecosystem, Tanzania and Kenya. Wildebeest annually move from the southern short-grass plains of the Serengeti to the northern woodlands of the Mara. We used satellite images to create 12 average monthly and 180 10-day surfaces from 1998 to 2003 of percentage rainfall and new vegetation. The surfaces were combined in five additive and three multiplicative models, with the weightings on rainfall and new vegetation from 0% to 100%. Modeled wildebeest were first assigned random migration pathways. In simulated generations, animals best able to access rainfall and vegetation were retained, and they produced offspring with similar migratory pathways. Modeling proceeded until the best pathway was stable. In a learning phase, modeling continued with the ten-day images in the objective function. The additive model, influenced 25% by rainfall and 75% by vegetation growth, yielded the best agreement, with a multi-resolution comparison to observed densities yielding 76.8% of blocks in agreement (kappa = 0.32). Agreement was best for dry season and early wet season (kappa = 0.22–0.57), and poorest for the late wet season (0.04). The model suggests that new forage growth is a dominant correlate of wildebeest migration.

Key words: Connochaetes taurinus; *evolutionary programming; migration; NDVI; rainfall estimates; Serengeti Mara Ecosystem; wildebeest.*

INTRODUCTION

Land use intensification has altered wildlife movements and migrations around the globe. Examples abound: forest clear-cutting reduced the probability of grizzly bears (*Ursus arctos*) crossing a watershed in Wyoming, USA (Boone and Hunter 1996); cultivation reduced movements of zebra (*Equus burchelli*) and wildebeest (*Connochaetes taurinus*) between Tarangire National Park and the Simanjiro Plains in northeastern Tanzania (Kahurananga and Silkiluwasha 1997); and Mongolian gazelles (*Procapra gutturosa*) appeared to be unwilling to cross railroad tracks (Ito et al. 2005). Ecologists charged with predicting effects of change on animal movements typically make estimates based upon their experience and knowledge, compare habitat suitabilities in spatial analyses or modeling (e.g., Serneels and Lambin 2001), or use cost-path or diffusion modeling (e.g., Boone and Hunter 1996). Long-term effects of landscape change on movement patterns are difficult to quantify using these methods, and many costs or permeability scores may be assigned, which can be subjective. Animal movement can include components of habitat selection, landscape permeability, *and* evolved, innate responses (Andersen 1991). Animal memory may be incorporated into diffusion models (Stamps and Krishnan 2001), but the resulting models can be complex. We used a straightforward optimization method called evolutionary programming to model a classic migration, the seasonal movement of ~1.3 million wildebeest in the Serengeti Mara Ecosystem. The method reflects constraints on movement because of innate responses, avoids the need for assignment of permeability to many land cover types, and includes long- and short-term optimization.

The Serengeti Mara Ecosystem

The Serengeti Mara Ecosystem (Fig. 1a) is defined by seasonal movements of the migratory wildebeest. Annual rainfall defines the seasons, with the wet season extending from about mid-October through April, and the dry season from May to mid-October. A strong gradient in annual rainfall exists, with rainfall >1000 mm/yr to the northwest and 450 mm/yr in the rain shadow of the Ngorongoro Highlands to the southeast. The rainfall gradient is mirrored by a vegetation gradient, with short-grass plains to the southeast, mid-grass plains and acacia woodlands in the central Serengeti, and tall grasses in the north. The western corridor of the Serengeti is more heavily wooded, and has taller grasses than in the east.

Wildebeest, zebra, and Thomson's gazelle (*Gazella thomsoni*) migrate within the Serengeti Mara Ecosystem.

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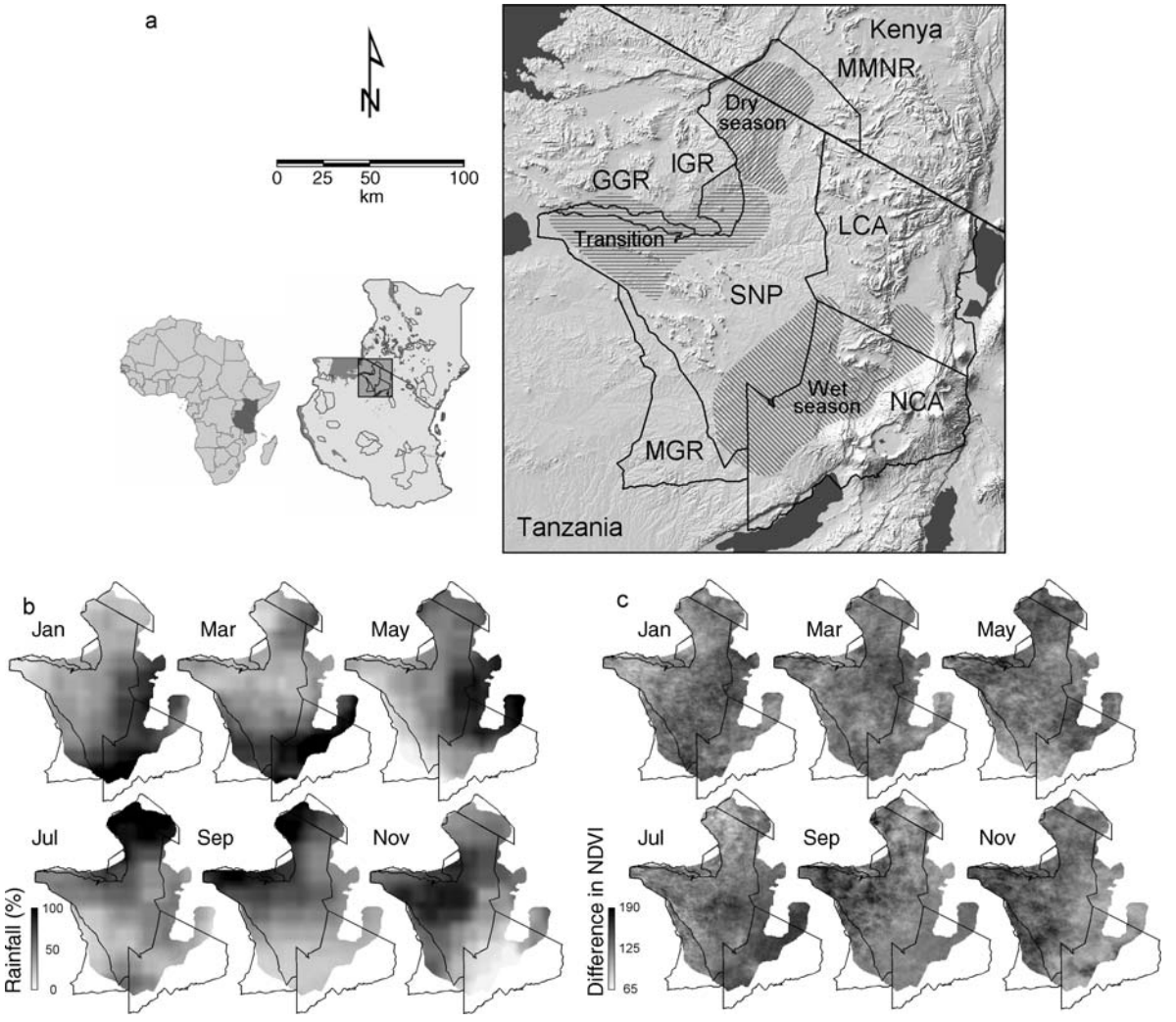

FIG. 1. The Serengeti Mara Ecosystem includes parts of northern Tanzania and southwestern Kenya (see insets). Areas include Serengeti National Park (SNP), Ngorongoro Conservation Area (NCA), Maswa Game Reserve (MGR), Masai Mara National Reserve (MMNR), Grumeti Game Reserve (GGR), Ikorongo Game Reserve (IGR), and Loliondo Controlled Area (LCA). (a) Wildebeest are in the northern portion of the ecosystem in the dry season, in the Western Corridor in transitional periods of some years, and in the southern part of the ecosystem in the wet season (adapted from Murray [1995] and Sinclair [1995]). (b) Mean distribution of rainfall as a percentage of the monthly total, and (c) difference in Normalized Difference Vegetation Indices (NDVI), where NDVI for a given month was subtracted from NDVI for a succeeding month to reflect plant growth, are shown for alternate months.

Wildebeest migrate in a roughly circular pattern (Fig. 1a). The pattern varies annually, but in the dry season the herds are in the northern Serengeti and Masai Mara National Reserve (Fig. 1a). As the rains return, the animals move south. In December, wildebeest are mostly in the short-grass plains of southern Serengeti National Park. Many move into the Ngorongoro Conservation Area, and give birth synchronously, with almost all calves being born in February and March (Estes 1976). As the wet season ends, wildebeest begin to move back toward the dry-season range, with some moving through the western corridor (Fig. 1a) (Thirgood et al. 2004).

At least 16 explanations have been given as to the cause or timing of wildebeest migration in the Serengeti ecosystem. These may be placed into six somewhat distinct categories entailing movement to access the following resources: (1) green forage (Jarman and Sinclair 1979) or rainfall leading to green forage (Talbot and Talbot 1963); (2) compensatory vegetative production (McNaughton 1976); (3) areas of fewer diseases or predators (Darling 1960, Fryxell and Sinclair 1988); (4) higher quality water (Gereta and Wolanski 1998); (5) minerals (Kreulen 1975, Murray 1995); and (6) resources synchronously, to reduce competition with resident ungulates and swamp predators during the calving season (Watson 1967, Estes 1976). The first category

of explanations, wherein wildebeest migrate to access green forage or follow rainfall leading to new green forage, is the focus of this paper.

Evolutionary programming

Evolutionary programming is a member of a group of optimization techniques known collectively as "evolutionary computation" and of a broader category called "soft computing." Evolutionary computation includes genetic algorithms, evolutionary strategies, genetic programming, and neural networks. These techniques share a foundation in biological principles, reflecting mutations and crossovers (genetic methods), strengthening of preferred pathways (neural networks), and natural selection. Evolutionary programming adopts features of natural selection, with four main steps. (1) Many potential solutions (i.e., offspring in natural selection) are generated, (2) the success of each solution is quantified (competition), (3) less successful solutions are removed (death), and (4) more successful solutions generate (birth) related (mutation) solutions that may be superior to the parents. This cycle may repeat for thousands of generations, with incrementally superior solutions selected, until the solution is sufficiently close to some ideal (e.g., using field observations) (Bentley and Corne 2002).

Although it is based upon ecological principles, evolutionary programming has been used much more often in engineering than ecology. Examples from biology are limited, but they include Koza et al. (1992) [J. R. Koza laid some of the foundation of the use of genetic programming in biology] and the GARP system (e.g., Peterson et al. 1999), which includes genetic programming and is used to predict ecological niches. In the mid-1990s, evolutionary computation was used to model fish life history and behavior (Huse and Giske 1998, Huse et al. 1999, Strand et al. 2002), and has recently been used to model movements of North American elk (*Cervus elaphus*; Morales et al. 2005). We used evolutionary programming to quantify the degree to which migratory wildebeest movements may be described using information on rainfall and new vegetation growth. Our modeling ranks the relative importance of these factors, and allows inference about other hypotheses related to wildebeest migration.

Methods

Data sources

The area used by migratory wildebeest is generally well defined. Mountains border the area to the southeast and east; agricultural areas are to the north; and there is an escarpment to the northwest. Hills border the Serengeti to the northwest, and to the southwest areas of dense cultivation border the national park. In a geographic information system (GIS), we began with the boundary defined by Sinclair (1995), and refined it using a relatively high-resolution digital elevation model (SRTM 2004) and a Landsat ETM+ mosaic (ESC 2004).

Simulated wildebeest responded to rainfall and new vegetation growth. The U.S. National Oceanic and Atmospheric Administration uses satellite images that contain cloud temperature and rainfall estimates to create African rainfall surfaces. About 1000 weather stations provide ground-based observations used to calibrate the satellite estimates (Xie and Arkin 1997). The surfaces have a resolution of 8×8 km and report estimated rainfall (millimeters) for 10-day periods ("dekades"), yielding 36 images per year. We acquired images for five years, May 1998 to April 2003 (ADDS 2004). The 180 images were imported into ArcInfo Version 8.1 (ESRI 2001), interpolated to 1-km resolution using cubic resampling (appropriate for floating-point spatial data), and trimmed to the ecosystem.

Based on hypotheses that wildebeest follow rainfall that leads to new vegetative growth (Talbot and Talbot 1963, Pennycuik 1975), we calculated surfaces that showed, for each pixel, the percentage of rainfall over a given year to fall within the given 10-day period. For each image, values were standardized based on the mean and standard deviation (mean $\pm$ 2 SD) to be between 1 and 255. Each image, (e.g., Fig. 1b), therefore had the potential to contribute a similar amount to the objective function, reflecting the logic that accessing areas of relatively heavy rainfall in the dry season was equally important to accessing areas of heavy rainfall in the wet season. We used analogous methods to create twelve monthly images averaged over the entire five-year period.

The second set of surfaces were Normalized Difference Vegetation Images (NDVI) from the SPOT Earth Observation System, developed by the Centre National d'Etudes Spatiales of France in cooperation with Sweden and Belgium (VITO 2002). They distribute images at 1×1 km resolution that represent maximum vegetation greenness over 10-day periods, so that each year includes 36 images. VEGETATION NDVI images for Africa were acquired from April 1998 to April 2003, the portion for the Serengeti subset, and imported into the spatial database.

Based on the hypothesis that wildebeest migratory patterns track nutritious, new, green forage (Jarman and Sinclair 1979), we calculated the change in NDVI between each period and the preceding period, yielding 180 difference images from May 1998 to April 2003. This difference highlighted areas of new vegetation growth. The images were standardized to contain values from 1 to 255 (mean $\pm$ 2 SD) (e.g., Fig. 1c). Finally, we calculated NDVI for each month, averaged across the five years, and then calculated the difference in greenness between months (including Dec–Jan), yielding monthly images analogous to the 10-day difference images. We did not account specifically for woody vegetation, which is prevalent in the western corridor of Serengeti, but taking the difference across NDVI images helped alleviate the problem. Areas that were green in both images received a neutral value. Despite the steps

involved in generating spatial surfaces, we will refer to the layers as simply rainfall or NDVI.

Evolutionary programming

Modeling proceeded in a two-stage process, generating a migratory pathway of an individual wildebeest for each simulation. These steps are in some ways analogous to two stages of adaptation: evolution and learning; we will adopt these terms. Evolution represents long-term adaptation to conditions across generations, whereas learning is short-term adaptations within an individual (Nolfi and Floreano 2000). In our evolutionary stage, a general cyclical annual migratory pathway evolved as animals responded to the 12 averaged rainfall and 12 averaged NDVI images. In the learning stage, the best-evolved migratory pathways initialized simulation of refined migratory patterns over the five-year period.

In the model, wildebeest movements were stored as vectors representing an individual's latitude and longitude within the Serengeti Mara Ecosystem, over 365 days for the evolutionary stage, and 1825 days for the learning stage. Nothing was included in pathways related to observed migration: initial pathways were entirely random. Initial annual pathways for each of the 250 animals in the population were generated by randomly identifying eight locations within the ecosystem, one every 46 days (8/365). The location of the wildebeest for the intervening days was calculated by interpolating between the vertices.

The attribute maximized by the migrating wildebeest (i.e., the objective function) was a function of rainfall and NDVI, accessed by the animal given its migratory route (pixels passed through by animals from one day to the next were ignored). The influence of these candidate surfaces was assessed using eight models: five additive models with the influence of rainfall from 0% to 100% and NDVI from 100% to 0% [i.e., (rainfall $\times$ 0.0 + NDVI $\times$ 1.0); (rainfall $\times$ 0.25 + NDVI $\times$ 0.75); (rainfall $\times$ 0.50 + NDVI $\times$ 0.50); (rainfall $\times$ 0.75 + NDVI $\times$ 0.25); (rainfall $\times$ 1.0 + NDVI $\times$ 0.0)], and three multiplicative (Fryxell 1991) models [i.e., (rainfall $\times$ 0.25 $\times$ NDVI $\times$ 0.75); (rainfall $\times$ 0.50 $\times$ NDVI $\times$ 0.50); (rainfall $\times$ 0.75 $\times$ NDVI $\times$ 0.25)]. For example, the additive objective function (O) where rainfall and NDVI were given equal weight was

$$O = \text{Maximize}\left[\sum_{i=1}^{\text{Days}} (\text{Rainfall} \times 0.50) + (\text{NDVI} \times 0.50)\right]$$

which quantified the degree to which wildebeest succeeded in accessing areas of both high rainfall and new vegetation. The general methods for the evolutionary stage of modeling, with biological analogs in brackets, were these: (1) scores were assigned to each of the 250 animals based on the objective function [competition]; (2) the half of the wildebeest population that scored the poorest was removed [mortality]; (3) the remaining half produced one offspring per animal [reproduction], with offspring movements the same as parents; (4) for each new offspring, a shift $\leq$2 km was added to each daily location [mutation] (mutations could not cause the animal to leave the ecosystem, or to travel $>$18 km in a day; Inglis 1976); (5) for a small number (10%) of the mutated animals, their starting point in the migratory cycle was altered to a random point within the existing pathway, and their paths may have been reversed; and (6) some (15%, or 38) mutated animals were replaced with new random pathways. Steps (5) and (6) were used to ensure that seasonality of movements was fitted in a timely way, and that a local optimum was not reached while a large part of environment space remained unsearched. Without step (5), for example, hundreds of thousands of generations may have passed before accumulated mutations resulted in a pathway that represented the general migratory cycle. These steps repeated until the pathway of the highest scoring wildebeest had not changed in 5000 generations.

After storing the evolved pathway generated during the evolutionary stage, the learning stage proceeded. The top scoring 25% of pathways were used (i.e., each four times) to populate vectors of movements representing 1825 days, with the 365-day evolved pattern repeated each year of the five-year period. The steps outlined were repeated in the learning stage, except that the 180 dekadal images were used to assign scores, and steps (5) and (6) were not used. When the locally optimum pathway was stable for 5000 generations, the simulation stopped.

The original evolutionary program (EPM) was written in Microsoft Visual Basic Version 6.0 (Microsoft, Redmond, Washington, USA), which included mapped output as pathways evolved. We modeled 100 pathways for each of the eight models assessed using a translation of the model in FORTRAN 90 (Lahey Computer Systems, Incline Village, Nevada, USA).

The simulated pathways from the evolving phase were compared to three data sets; data from real wildebeest were not sufficient to assess the yearly pathways created during the learning phase. The statistical comparison was to migratory wildebeest occurrences recorded for 5 $\times$ 5 km blocks during aerial surveys from 1969 to 1972 (data collected by M. Norton-Griffith and summarized in Maddock 1979), summarized as monthly distributions using four ranks, with the last two ranks (250-2500 and 2500–25 000 animals) used here. We used a multiple-resolution procedure to test goodness of fit (Costanza 1989, Kuhnert et al. 2005). For each model, we created monthly density grids at 5 $\times$ 5 km resolution representing the locations of simulated wildebeest on the 15th day of the month and discarded low densities. We then compared the modeled and observed distributions, tallying blocks that agreed and disagreed, and calculating a kappa statistic (Cohen 1960). The resolution of the maps were reduced to 10 $\times$ 10, 25 $\times$ 25, and 50 $\times$ 50 km square blocks, and comparisons repeated. Finally, a

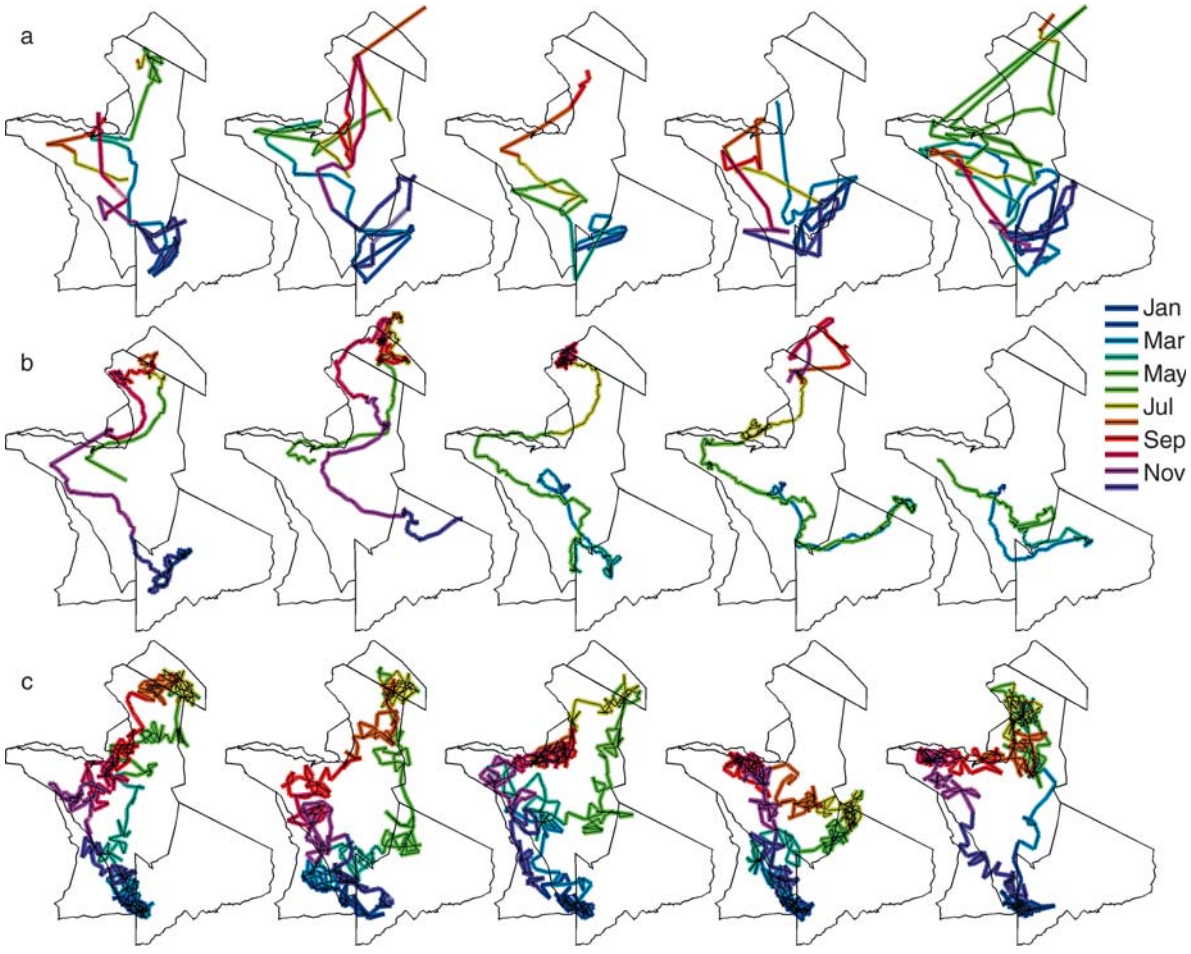

FIG. 2. Pathways from (a) five VHF-tracked wildebeest, (b) five GPS-tracked wildebeest, and (c) five simulated wildebeest. Lines connect successive observations of tracked animals that are typically more than one day apart and do not indicate direct travel between points.

small number of simulated pathways were selected haphazardly, and compared visually to the observed pathways of individual wildebeest collected using VHF telemetry (1971–1973) and GPS collars (1999–2001).

RESULTS

In the evolutionary stage of simulations, a simple (i.e., eight vertices), but reasonable migratory pathway evolved in fewer than 10 generations. Thousands more generations passed as that pathway slowly evolved to a local optimum, then the learning phase proceeded. For the 100 pathways simulated for each of the eight models, the evolved, annual migratory pathways were finalized after almost 40 000 generations (mean = 39 890, SD = 14 209, including 5000 generations where the pathway did not change). Learned pathways, simulated using dekadal surfaces, were finalized after thousands more generations (mean = 36 957, SD = 13 989, including 5000 generations where the pathway did not change). Different objective functions yielded very different total scores accessed by the modeled wildebeest, but the deviation between animals was low (e.g., from mean = 53 084 with SD = 431.4 to mean = 2 779 520 with SD = 90 512 during the evolving stage of modeling).

Simulated pathways evaluated visually appear to resemble pathways of individually tracked wildebeest reasonably well (Fig. 2). The additive model with 75% influence from NDVI and 25% from rainfall had the highest agreement with observed monthly distributions (i.e., in summaries of multiple-resolution comparisons, the agreement in presence or absence was 76.8%, presence only was 37.0%, and kappa was 0.32; Appendix A presents comparison results from the eight models; Appendix B shows the monthly distributions from the evolutionary stage of simulation for each of the models.) Overall fit was fair, based on kappa (Landis and Koch 1977). At the finest resolution of the observed data, 83% of blocks were correctly classified as present or absent through the year, and 13.4% of blocks with wildebeest observed or predicted to be present agreed (Fig. 3). Agreement was not equal across months, however (i.e., kappa for January–March: 0.57, 0.49, 0.56; April–June: 0.04, 0.15, 0.16; July–September: 0.10, 0.44, 0.39; October–December: 0.35, 0.22, 0.30). From the learning

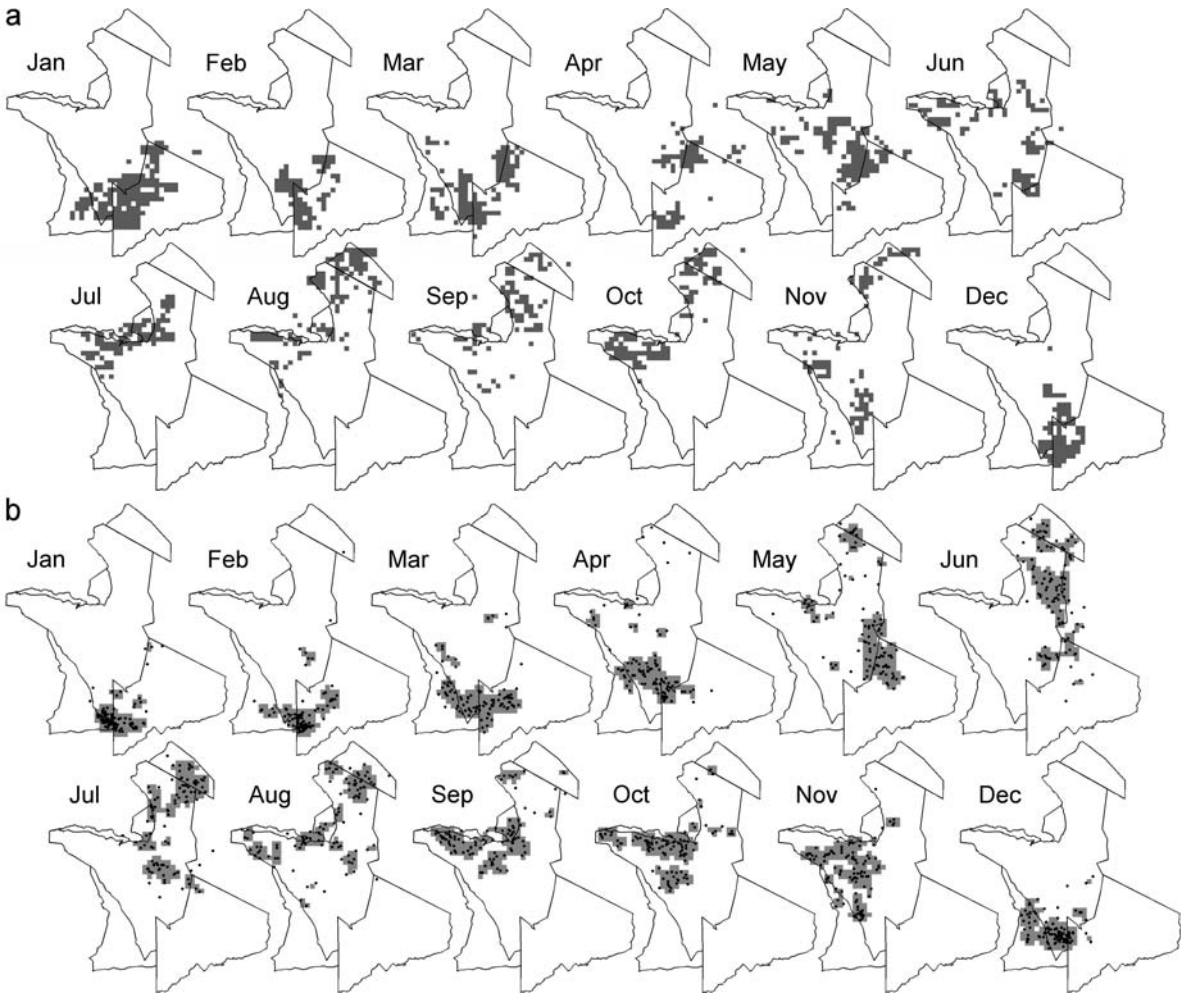

FIG. 3. (a) The average monthly distributions of wildebeest in 1969–1972, with ≥250 animals in a 5 × 5 km block. These may be compared with (b) the average monthly distribution of simulated wildebeest from the additive model that included 75% influence from NDVI and 25% from rainfall. Blocks with low densities of occurrences were discarded. In (b), the blocks of simulated wildebeest on the 15th day of each month are shown as dots, and blocks used in the assessment are shaded light gray.

stage of modeling, simulated pathways overlapped between years in the wet and dry season, but pathways sometimes deviated 15 km or more from the evolved pathway (see Appendix C for nine evolved pathways, and their yearly pathways for 1999–2002).

DISCUSSION

The relatively close agreement between reported and simulated migratory pathways suggests that new forage growth and rainfall are dominant correlates of the migratory pattern (Talbot and Talbot 1963, Jarman and Sinclair 1979, Wilmshurst et al. 1999). Although the evidence is essentially through correlation, it appears that "[i]n this system of migratory herbivores … a pasture rotation system has evolved naturally in relation to seasonal rainfall patterns" (McNaughton 1979). We believe that rainfall drives the general north–south migration, but using rainfall alone in modeling yielded too many animals moving into the Masai Mara, for example (Appendix B). New forage growth in heterogeneous patches, reflected in NDVI (Fig. 1c), dispersed the animals and kept them farther south in the dry season, as in the observed data. Other correlates identified or hypothesized, such as water quality (Gereta and Wolanski 1998), avoidance of disease and predators (Darling 1960, Talbot and Talbot 1963, Fryxell et al. 1988), or access to minerals (Kreulen 1975, Maddock 1979, Murray 1995) may be important locally or subdominant across the ecosystem. That said, some correlates, such as compensatory growth of vegetation (McNaughton 1976), may be included in the greenness indices used in modeling.

Although the simulated wildebeest pathways agree fairly well with some in reality, they included considerable variation (Fig. 2). As in nature, some wildebeest moved into the Masai Mara National Reserve in the dry season and some stayed within Serengeti National Park. Some wildebeest entered the Ngorongoro Conservation

Area in the wet season and some remained in the short grass plains of the southern Serengeti (Thirgood et al. 2004). In general, the simulated wildebeest moved quickly in transition areas and slowly in the wet- and dry-season ranges, as seen in collared individuals (Inglis 1976, Thirgood et al. 2004). With the caveats that surfaces used in modeling (1998–2003) and observed density estimates (1969–1972) are separated by 30 years, and that there were fewer wildebeest at the time of the surveys, agreement is poorest in the late wet season, and the transitional period into the dry season (April through July). Simulated wildebeest moved to the northwest in April, whereas in the observed seasons, wildebeest remained in Ngorongoro or moved to the northeast (Fig. 3). Rainfall was greater and in a steeper gradient in 1969–1972 than in 1998–2003 (J. G. C. Hopcraft, *unpublished data*), which may explain why wildebeest stayed in the south longer in the observed data. In simulations, more animals moved through Loliondo Game Controlled Area, compared to the maps from Maddock (1979); incorporating topography may have reduced the number of wildebeest moving through more topographically diverse Loliondo. Sinclair (1995) has noted, however, that in recent decades wildebeest have been moving through Loliondo more often, and in the observation data used here, many animals were in eastern Serengeti in June (Fig. 3). The inclusion of surfaces related to other correlates of hypotheses of migration cited above (e.g., water quality, disease, predators) would likely improve agreement with observed data.

The logic used in our modeling should allow migratory pathways over the five-year period to have evolved using a single stage of modeling and the dekadal images. However, in exploratory analyses, we found that reasonable patterns would not evolve in many thousands of generations. Small mutations that built incrementally toward the complex five-year migratory pattern were not identified or allowed to produce offspring. If one wished to use a single stage, rather than the two stages of modeling we used here, it is likely that some method of identifying and preserving reasonable incremental changes within years would need to be developed.

Here we have used a lengthy terrestrial migration, but evolutionary programming and other soft-computing methods may be used across scales to model, for example, movements of fishes within water columns (small-scale) (Huse et al. 1999, Strand et al. 2002), ungulates moving seasonally between ranges (medium-scale) (Morales et al. 2005), or birds migrating annually between continents (large scale). The surfaces used to evolve movement patterns may be altered in experiments or may include results from simulations (e.g., climate model surfaces), assuming that important relationships between biophysical data and species can be identified (Turchin 1998, Scott et al. 2002). The difference in movements evolved in the two sets of simulations may be compared to quantify the effects of some change (e.g., global climate change). For example, Boone and Hunter (1996) explored the likelihood that grizzly bears would cross a watershed with clearcuts in place. Movement across the watershed could be modeled using evolutionary programming, then the surfaces (e.g., forest cover) edited to reflect clear-cuts. After re-evolving movements, the effects of the clear-cuts on movements would be quantified.

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APPENDIX A

Measures of goodness-of-fit for wildebeest pathways from eight objective functions averaged for multiple-resolution comparisons from 5 to 50 km square blocks (*Ecological Archives* E087-124-A1).

APPENDIX B

Locations on the 15th of each month of wildebeest simulated in the evolutionary stage for models influenced by rainfall and new vegetation growth, as reflected in NDVI (*Ecological Archives* E087-124-A2).

APPENDIX C

Nine wildebeest migratory pathways that evolved using average monthly surfaces in the additive model, and yearly pathways refined in a learning phase (*Ecological Archives* E087-124-A3).